7

Fishes of the Lower Klamath Basin

Native fishes of the lower Klamath basin are mainly anadromous species that use productive flowing-water habitats and a few nonmigratory stream fishes typical of cool-water environments. Because the watershed has been drastically altered by human activities, it has become progressively less favorable for anadromous fishes, including coho salmon. Given that the native anadromous fishes support important tribal, sport, and commercial fisheries and have high iconic value, there is widespread support among stakeholders, both inside and outside the basin, for restoration of these fishes to their earlier abundances. Restoration efforts would most rationally apply to all native fishes, not just those listed or proposed for listing under the federal Endangered Species Act (ESA). If broadly based restoration does not occur, additional anadromous species are likely to be listed under state and federal endangered species acts. Furthermore, because actions that are perceived to benefit one species may do harm to another, the species cannot be treated as isolated units.

The lower Klamath basin supports 19 species of native fishes (Table 7-1). Thirteen (68%) of the 19 are anadromous, and two are amphidromous (larval stages in salt water); thus, 80% of the fishes require salt water to complete their life histories. The remaining four species spend their life entirely in fresh water and show close taxonomic ties to fishes in the upper basin or adjacent basins. The species composition of native fishes supports geologic evidence that the Klamath River in its present form is of relatively recent origin. One of the resident fishes (the lower Klamath marbled sculpin), however, is distinctive enough to be recognized as a subspecies and several of the anadromous species have distinct forms adapted to the special conditions of the Klamath basin.

In addition, 17 nonnative species of fishes have been recorded in the basin (Table 7-2); only two of these are anadromous. For the most part, these fishes are confined to human-created environments—such as reservoirs, ponds, and ditches—although individuals constantly escape into the streams, where they may take advantage of favorable habitats created by human activity. In addition, nonnative fishes come down continually from the upper Klamath basin.

Table 7-1. Native Fishes of the Lower Klamath River and Its Tributaries

Name [a]	Life History	Status in Lower Klamath and Trinity Rivers[a]	Comments
Pacific lamprey, *Lampetra tridentata*	A	Declining	TTS, probably multiple runs
River lamprey, *L. ayersi*	A	Uncommon	Poorly known
Klamath River lamprey, *L. similis*	N	Common	Poorly known
Green sturgeon, *Acipenser medirostris*	A	State special concern, proposed for listing	TTS, important fishery
White sturgeon, *A. transmontanus*	A	Uncommon	May not spawn in river
Klamath speckled dace, *Rhinichthys osculus klamathensis*	N	Common, widespread	Most widespread fish in basin
Klamath smallscale sucker, *Catostomus rimiculus*	N	Common, widespread	Found also in Smith and Rogue rivers
Eulachon, *Thaleichthys pacificus*	A	State special concern	TTS, huge runs now gone, lowermost river only
Longfin smelt, *Spirinchus thaleichthys*	A	State special concern	Small population mainly in estuary
Prickly sculpin, *Cottus asper*	Am	Common	Larvae wash into estuary
Coastrange sculpin, *C. aleuticus*	Am	Common	Larvae wash into estuary
Lower Klamath marbled sculpin, *C. klamathensis polyporus*	N	Common?	Endemic
Threespine stickleback, *Gasterosteus aculeatus*	A/N	Common	Migratory close to ocean, anadromous; upstream forms nonmigratory
Coho salmon, *Oncorhynchus kisutch* Southern Oregon-Northern California ESU	A	Federally threatened	Being considered for state listing, TTS
Chinook salmon, *O. tshawytscha*			TTS
Southern Oregon-Northern California ESU	A	Commonest salmon below mouth of Trinity River	Much reduced in numbers
Upper Klamath and Trinity rivers ESU			
Fall run	A	Commonest salmon in both rivers	Much reduced, focus of hatcheries
Late fall run	A	Possibly extinct	Presence uncertain
Spring run	A	Endangered but not recognized as ESU	Distinct life history, adults require cold water in summer
Chum salmon, *O. keta*	A	Rare, state special concern	Southernmost run of species, TTS
Pink salmon, *O. gorbuscha*	A	Extinct	Breeding in basin poorly documented, TTS
Steelhead (rainbow trout), *O. mykiss* Klamath Mountains Province ESU	A, N	Common but declining; proposed for listing	Resident populations above barriers, TTS
Winter run	A	Most abundant	Distinct life history
Summer run	A	Endangered but not recognized as separate ESU	Distinct life history, adults require cold water in summer
Coastal cutthroat trout, *O. clarki clarki*	A, N	State special concern	Only in lower river and tributaries, resident populations above barriers, TTS

[a]Evolutionarily significant unit.
Abbreviations: A, anadromous; Am, amphidromous; N, non-migratory; TTS, tribal trust species.

Table 7-2. Nonnative Fishes of the Lower Klamath and Trinity Rivers

Name	Life History	Status	Comments
American shad, *Alosa sapidissima*	A	Uncommon	Small annual run in lowermost reach of river
Goldfish, *Carassius auratus*	N	Uncommon	Ponds and reservoirs
Fathead minnow, *Pimephales promelas*	N	Uncommon	Invading from upper basin where extremely abundant
Golden shiner, *Notemigonus chrysoleucas*	N	Uncommon	Important bait fish in California
Brown bullhead, *Ameiurus nebulosus*	N	Locally abundant	Ponds and reservoirs, especially Shasta River; some in mainstem
Wakasagi, *Hypomesus nipponensis*	N	Locally abundant	In Shastina Reservoir but a few downstream records
Kokanee, *Oncorhynchus nerka*	N	Locally abundant	Reservoirs
Brown trout, *Salmo trutta*	N, A	Common in some streams	Sea-run adults rare
Brook trout, *Salvelinus fontinalis*	N	Common	Only in headwater streams and lakes
Brook stickleback, *Culea inconstans*	N	Locally abundant, spreading	Recent introduction into Scott River
Green sunfish, *Lepomis cyanellus*	N	Common	Warm streams, ditches, and ponds
Bluegill, *L. macrochirus*	N	Common	Ponds and reservoirs
Pumpkinseed, *L. gibbosus*	N	Uncommon	Abundant in upper basin
Largemouth bass, *Micropterus salmoides*	N	Common	Ponds and reservoirs
Spotted bass, *M. punctulatus*	N	Locally common	Only in Trinity River reservoirs
Smallmouth bass, *M. dolomieui*	N	Locally common	Only in Trinity River reservoirs
Yellow perch, *Perca flavescens*	N	Locally common	Abundant in upper basin, including Iron Gate Reservoir

Abbreviations: A, anadromous; N, non-migratory.

COHO SALMON

The coho salmon (Figure 7-1) once was an abundant and widely distributed species in the Klamath River and its tributaries, although its historical numbers are poorly known because of the dominance of Chinook salmon. Snyder (1931) reported that coho were abundant in the Klamath River but also indicated that reports of the salmon catch probably lumped coho and Chinook. Historically, coho salmon occurred throughout the Klamath River and its tributaries, at least to a point as high up in the system as the California-Oregon border. It is possible that they once migrated well into the upper Klamath basin (above Klamath Falls), as did Chinook and steelhead, but there are no records of this, perhaps because most people are unable to distinguish them (Snyder 1931).

Today coho salmon occupy remnants of their original range wherever suitable habitat exists and wherever access is not prevented by dams and diversions (Brown et al. 1994, Moyle 2002). Because the coho salmon is clearly in a long-term severe decline throughout its range in California, all populations in the state have been listed as threatened under both state and federal endangered species acts (CDFG 2002).

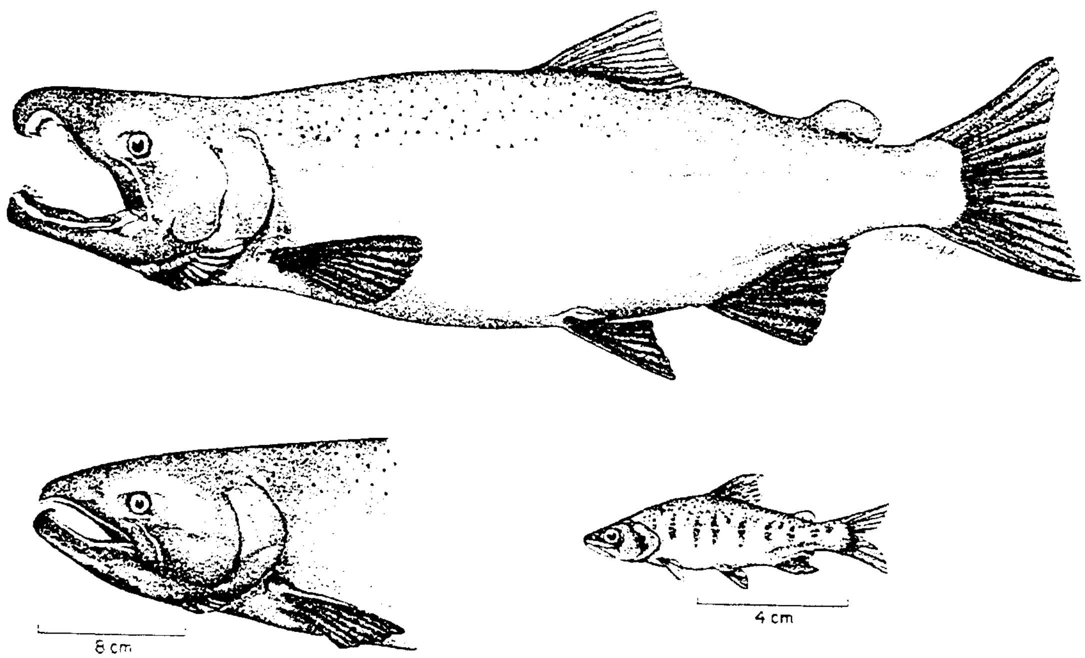

Figure 7-1. Coho salmon male (top), female (head), and parr. Source: Moyle 2002, permission pending. Drawing by Chris M. Van Dyck.

Life History

Coho salmon in the Klamath basin have a 3-yr life cycle (3 yr is the time from spawning of a parent to spawning of its progeny), about the first 14-18 mo of which is spent in fresh water, after which the fish live in the ocean until they return to fresh water to spawn at the age of 3 yr. The main variation in the cycle is that a small percentage of the males return to fresh water to spawn early (in their second year, before spending a winter at sea) as "jacks." A few juveniles may also remain in fresh water for 2 yr (e.g., Bell et al. 2001), although this has not been documented for Klamath basin coho. Adults typically start to enter the river for spawning in late September. They reach peak migration strength between late October and the middle of November. A few fish enter the river through the middle of December (USFWS, unpublished material, 1998). Adult coho generally enter streams when water temperatures are under 16°C and rains have increased flows (Sandercock 1991). The presence, however, of small numbers of adult coho in the fish kill of September 2002, indicates that some coho begin migration without these stimuli. Most spawning takes place in tributaries, especially those with forested watersheds, but some mainstem spawning has been recorded (Trihey and Associates 1996). Spawning usually takes place within a few weeks of the arrival of fish in the spawning grounds. Females dig redds (nests) in coarse gravel and spawn repeatedly with large, hooknose males and with small jacks over a period of a week or more. The fertilized eggs are covered with gravel after each spawning event. Adults die after spawning.

Embryos develop and hatch in 8-12 wk, depending on temperature. Alevins (hatchlings with yolk sacs attached) remain in the gravel for another 4-10 wk (Sandercock 1991). In forested watersheds with relatively stable slopes and stream channels, mortality is lower for embryos and alevins than it is in disturbed watersheds (Sandercock 1991). Major sources of mortality include scouring of redds by episodes of exceptionally high flow and smothering of embryos by silt. When most of the yolk sac is absorbed, the alevins emerge from the gravel as fry (30-35 mm) and seek the shallow stream margins, where velocities are low and small invertebrates are abundant. Fry start emerging in late February and typically reach peak abundance in March and April, although fry-sized fish (up to about 50 mm) appear into June and early July (CDFG, unpublished data, 2000, 2001, 2002). Fry are nonterritorial and have a tendency to move around (Kahler et al. 2001); this allows them to disperse. Thus, some fry are captured in outmigrant traps at the mouths of the Shasta and Scott rivers from May to early July (CDFG, unpublished data, 2000, 2001, 2002), although most probably stay in the tributaries close to the areas in which they were spawned.

There is no sharp separation between fry and juvenile (parr) stages; juveniles are typically over about 50-60 mm and partition available habitat among themselves through aggressive behavior (Sandercock 1991). Juveniles develop in streams for a year. Typical juvenile habitat consists of pools and runs in forested streams where there is dense cover in the form of logs and other large, woody debris. They require clear, well-oxygenated water and low temperatures. Preferred temperatures are 12-14°C, although juvenile coho can under some conditions live at 18-29°C for short periods (McCullough 1999, Moyle 2002). For example, Bisson et al. (1988) planted juvenile hatchery coho in streams that had been devastated by the eruption of Mount St. Helens 3-4 yr earlier and found that they showed high rates of growth and survival in areas where maximum daily temperatures regularly exceeded 20°C and occasionally reached 29°C. Early laboratory studies in which juvenile coho were reared under constant temperatures indicated that exposure to temperatures over 25°C, even for short periods, should be lethal (Brett 1952). But laboratory studies in which temperatures were increased gradually (for example, 1°C/h) suggest that lethal temperatures range from 24 to 30°C, depending on other conditions and the temperature to which the fish were originally acclimated (McCullough 1999). In the laboratory, juvenile coho can be reared at constant temperatures of 20-23°C if food is unlimited (McCullough 1999); but in hatcheries, they typically are reared at lower temperatures because of their reduced growth and increased mortality from disease at higher temperatures. Coho at Iron Gate Hatchery are reared at summer temperatures near 13-15°C (Bartholow 1995).

Consistent with the experiences of hatcheries, most coho develop and grow where water temperatures are at or near the preferred temperatures for much of each 24-hr cycle. For example, in tributaries to the Matolle River, California, Welsh et al. (2001) found that juveniles persisted through the summer only in tributaries where the daily maximum temperature never exceeded 18°C for more than a week. In the Klamath basin, such suitable conditions exist today mainly in portions of tributaries that are not yet excessively disturbed (Figure 1-1). NMFS (2002) has identified, in addition to the Shasta, Scott, Salmon, and Trinity rivers, six creeks between Iron Gate Dam and Seiad Valley, 13 creeks between Seiad Valley and Orleans, and 27 creeks between Orleans and the mouth of the Klamath as important coho habitat in the Klamath basin.

The explanation of seemingly contradictory information on temperature tolerance lies in the realm of bioenergetics. Juvenile coho can survive and grow at high daily maximum temperatures provided that (1) food of high quality is abundant so that foraging uses little energy and maximum energy can be diverted to the high metabolic rates that accompany high temperatures, (2) refuge areas of low temperature are available so that exposure to high temperatures is not constant, and (3) competitors or predators are largely absent so that the fish are not forced into physiologically unfavorable conditions or energetically expensive behavior (such as aggressive interactions). Thus, in the streams around Mount St. Helens cited above, food was abundant and temperatures were low much of the time. Temperatures dropped well below 15°C at night even after the hottest summer days, were below 16°C for 65-80% of the time, and rarely exceeded 25°C (Bisson et al. 1988). There were also areas of cool groundwater inflow that served as refuges on hot days, although the extent of their use by coho was not documented. And coho were the only species present. In some rivers, however, interactions of coho with juvenile Chinook and steelhead cause shifts of coho into energetically less favorable conditions (Healey 1991, Harvey and Nakamoto 1996). For example, coho juveniles occupying tributaries at the Matolle River faced not only limited food supplies but also energetically expensive interactions with juvenile steelhead (Welsh et al. 2001) and so were restricted to cool water.

Observations of juvenile coho in the mainstem Klamath River during summer suggest that juvenile coho live in the main stem despite temperatures that regularly exceed 24°C and are usually over 20°C for much of the day from late June through the middle of September (M. Rode, CDFG, personal communication, USFWS, unpublished data, 2002). Temperatures at night typically drop to 18-20°C during the warmest period. The coho occupy mainly pools at the mouths of inflowing streams where temperatures are usually 2-6°C lower than the water in the main river. The pools apparently are the only cool-water refugia in the river and occupy only a small area (B. A. McIntosh and H. W. Li, unpublished report, 1998). The coho in the pools appear to move into warmer water to forage on the abundant aquatic insects (D. Hillemeier, Yurok Tribe, personal communication). Thus, it is at least possible that coho could, from a bioenergetic perspective, occupy the main stem. Snorkel surveys of mouth pools in 2001 show, however, that juvenile coho, in contrast with Chinook and steelhead, occupied 16% of the tributary-mouth pools in June but only a single pool in August and September (T. Shaw, USFWS, unpublished material, 2002; Table 7-3).

Most of the tributary mouth pools contain juvenile Chinook salmon, steelhead, or both (Table 7-3). These fishes can compete with and prey on juvenile coho (and each other) and are somewhat more tolerant of high temperatures than coho. While many of these juveniles resulted partly from natural spawning, many of them likely came from Iron Gate Hatchery. Many large (70-90 mm) juvenile Chinook from the hatchery move down the river from late May through July, as do large numbers of hatchery steelhead smolts in March and April. Interactions among hatchery and wild fish of all species may cause wild fish, which are smaller, to move downstream prematurely when cool-water habitat becomes limiting in summer, although this possibility has not been documented for the Klamath River. The number of pools occupied

Table 7-3. Pools Containing Juvenile Coho Salmon, Chinook Salmon, and Steelhead Along Main Stem of Klamath River, 2001, as Determined in Snorkeling Surveys[a]

Month of Survey	No. of Mouth Pools Surveyed	No. (%) of Pools with Juvenile Fish		
		Coho	Chinook	Steelhead
June	31	5 (16)	26 (84)	26 (84)
July	46	7 (15)	41 (89)	43 (93)
August	39	1 (3)	26 (67)	34 (87)
September	32	1 (3)	13 (41)	28 (88)

[a]The data are comprehensive in that they include all tributaries large enough to form a cool pool, and include some tributaries below the Trinity River (e.g., Blue Creek).
Source: T. Shaw, USFWS, unpublished material, 2002.

by Chinook salmon declines by August and September, as does the number of Chinook present in each pool that has fish (T. Shaw, USFWS, unpublished material, 2002); this reflects the normal outmigration of both wild and hatchery juvenile Chinook. Steelhead remain in most pools throughout the summer.

Although 2001 was a year of exceptionally low flows, Table 7-3 suggests that coho juveniles are uncommon in the main stem in early summer and become progressively less common as the season progresses. Juvenile coho are virtually absent from the main stem, including pools at tributary mouths, by late summer, even though juvenile Chinook and steelhead persist in these habitats. Although the overall rarity of coho in the Klamath basin may contribute to their absence from the mouth pools, their presence early in the summer and the reduced densities of juvenile Chinook salmon as summer progresses suggest that juvenile coho would be noticed by observers in late summer if they were present. In one respect, the near absence of coho by late summer is surprising because juvenile coho do move about and should be continually dropping into the pools from tributaries (Kahler et al. 2001). Movement of coho juveniles may be prevented by the warming or drying of the lower reaches of tributaries in late summer.

Overall, it appears that the bioenergetic demands of juvenile coho prevent them from occupying the main stem. Even with abundant food, the thermal refugia (the pools at mouths of tributaries) are inadequate: nighttime temperatures stay too high for them, and the energy costs of interactions with Chinook and steelhead, both of which are much more abundant in the pools, are probably high. Coho juveniles in the pools during June and July may die by late summer. Alternatively, they could be moving back into tributary streams, but temperatures in the lower reaches of the tributaries are similar to those of the mouth pools by late summer, and barriers to reentry (such as gravel bars) are often present. It is also possible that coho juveniles move to the estuary, perhaps traveling at night, when temperatures are lowest. Estuarine rearing of juvenile coho has been documented in other systems (Moyle 2002). A rotary-screw trap set near Orleans on the lower river for 10 yr (1991-2001) caught juvenile coho from April through July, after which the trap was taken from the river; peak numbers were observed in May and June—5 times higher than in July (T. Shaw, USFWS, unpublished data). Annual seining data from the estuary (1993-2001) indicate, however, that coho are absent from the estuary or are very rare from July through September, when temperatures often exceed 18°C (M. Wallace, CDFG, unpublished memorandum, 2002). Thus, the evidence points to the conclusion that juvenile coho are not occupying either the estuary or the main stem through the summer.

One proposal for increasing the survival of juvenile coho in the main stem in summer has been to release more water from Iron Gate Reservoir to increase the habitat for juvenile coho, as defined by analogy with habitat used by juvenile Chinook salmon, and to reduce daily temperature fluctuations in the river, thus removing the potentially lethal temperature peaks (Chapter 4). The water available from Iron Gate Reservoir, however, is quite warm in summer (18-22°C or more) and, because it is increasingly warm as it moves downstream, is unlikely to ameliorate high temperatures very much. Modeling suggests that additional flows may indeed reduce maximum temperatures some distance downstream but that they will also increase minimum temperatures (Chapter 4). From a bioenergetic perspective, increasing minimum temperatures may be especially unfavorable for coho in the main stem because nocturnal relief from high temperatures would be reduced.

The low abundance of juvenile coho in the main stem in summer, the known thermal regimes of the main stem, and the bioenergetic requirements of coho together suggest that the most crucial rearing habitat for juveniles is that of cool tributaries. Today, cool tributaries are mainly small streams that flow directly into the Klamath or into the Shasta, Scott, Salmon and Trinity rivers. With its large, cold springs in the headwaters, the entire Shasta River was probably once favorable habitat for coho juveniles in most years, but diversions and removal of riparian vegetation have made it generally lethal thermally for salmonids in summer. If warming occurs with future climate change, it would likely exacerbate other factors that have led to warming of the tributaries (see Chapter 8).

Even a stream that has suitable summer habitat for juvenile coho may be unsuitable in winter. Studies in Oregon and elsewhere indicate that overwintering habitat is a major limiting factor where summer conditions are favorable (Nickelson et al. 1992a, b). Juveniles need refuges from winter peak flows. The refuges are side channels, small clear seasonal tributaries, logjams, and other similar areas. Simplification of channel structure through removal of woody debris or channelization eliminates much of the overwintering habitat. The condition of winter habitat for coho in the Klamath basin has not been evaluated.

Barred juveniles (parr) transform into silvery smolts and begin migrating downstream in the Klamath basin between February and the middle of June (USFWS, unpublished material, 1998) when they are about 10-12 cm long. Most smolts captured in the Orleans screw trap are taken in April and May (T. Shaw, USFWS, unpublished material, 2002) and appear in the estuary at about the same time (M. Wallace, CDFG, unpublished memorandum, 2002). Typically, coho smolts migrate downstream on the declining end of the spring hydrograph. About 60-70% of the smolts are of hatchery origin (M. Wallace, CDFG, unpublished memorandum, 2002). They are largely gone from the estuary by July. The transformation of juveniles into smolts appears to be triggered by light (perhaps moonlight) and other changing environmental conditions. Smoltification results in profound physiological and morphological changes in the fish. Smolts are compelled to move to the marine environment and will actively swim downstream to do so, especially at night. Exact timing of the downstream movement appears to be affected by flow, temperature, and other factors (Sandercock 1991). Higher flows in the river in April and May probably decrease transit time of the smolts. Low transit time could reduce predation rates and reduce energy consumption in swimming, although this has not been demonstrated in the Klamath River.

Smolts may feed and grow in the estuary for a month or so before entering the ocean (e.g., Miller and Sadro 2003). Coho entering the ocean generally have their highest mortality rates in their first few months at sea (Pearcy 1992). The first month or so after entry may be especially important due to predation, which suggests that smolts will have higher survival rates if they are large before going out to sea (C. Lawrence, UCD, personal communication, 2002). Once at sea, they spend the next 18 mo or so as immature fish that feed voraciously on shrimp and small fish, and grow rapidly.

Ocean survival depends on a number of interacting factors, including the abundance of prey, density of predators, the degree of intraspecific competition (including that from hatchery fish), and fisheries (NRC 1996). The importance of these factors in turn depends on ocean conditions (productivity, predation, and other factors), which vary widely on both spatial and temporal scales. Even relatively small changes in local and annual fluctuations in temperature, for example, can be related to changes in salmon survival rates (Downton and Miller 1998). Even more important are multidecadal (20-50 yr) fluctuations in ocean conditions, which can result in drastic changes in ocean productivity for extended periods of time (Hare et al. 1999, Chavez et al. 2003). Prolonged climatic shifts have caused significant shifts in salmonid populations to the north or south through modification of ocean temperatures (Ishida et al. 2001). Global warming thus could result in a shift in salmonid distribution to the north, and cause an overall decrease in abundance of salmonids (Ishida et al. 2001).

When the ocean is in a period of low productivity, survival rates may be low, and thus result in reduced runs coming into the streams. Commercial fishing is most likely to affect salmon populations during periods of naturally low ocean survival, but the fishery for wild coho salmon has been banned in California since 1997 and the fishery for Chinook has been greatly reduced (Boydstun et al. 2001). A fishery for coho still exists off the Oregon coast, but only hatchery fish, which are marked, can be retained.

Historically, the abundance of coho spawners reflected a balance between ocean survival and freshwater survival (Figure 7-2). A year of especially poor conditions for survival in fresh water (e.g., created by drought) could be compensated for if conditions in the ocean (e.g., high regional productivity: Hobday and Boehlert 2001) enhanced survival there. Persistently poor conditions in fresh water, such as exist throughout the Klamath basin today, make the recovery of populations difficult, however, even when ocean conditions are favorable and fisheries have been shut down or reduced. When ocean conditions are poor, the positive effects of restoring of salmonid habitat in streams may be masked (Lawson 1993, NRC 1996). Thus, only long-term monitoring can reveal effects of restoration.

Hatcheries

Coho salmon have been an important part of the Klamath basin fish fauna since prehistoric times (CDFG 2002), and many attempts have been made to augment their populations in the Klamath basin. The first attempt occurred in 1895, when 460,000 fish from Redwood Creek—part of the same evolutionarily significant unit (ESU) as Klamath River coho—

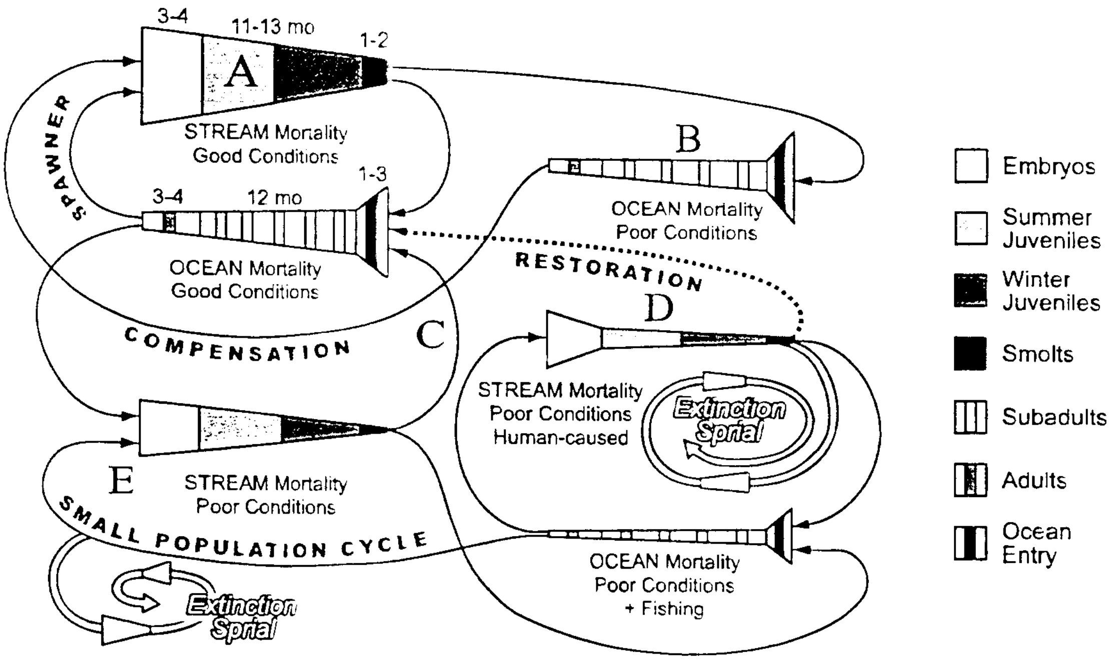

Figure 7-2. Population cycles of coho salmon in California. If conditions are favorable in spawning and rearing streams (A) and conditions are also favorable for high survival rates in the ocean, large populations of salmon will result. Even if conditions for survival are relatively poor in the ocean (B), large populations of coho may be maintained (although not as well as in cycle A) as long as production of coho in fresh water is high. Likewise, poor conditions in fresh water from natural causes (C) can be partially compensated for if ocean survival rates are high. If coho streams are degraded by human activity (D) and ocean conditions are poor, combined mortality may result in downward spiral of population size. If conditions in both fresh and salt water result in low survival (E), extinction may occur. Source: based on information in Moyle 2002.

were stocked in the Trinity River. It is not known whether these fish, which were taken from a small stream, survived and contributed to later populations. Hatchery production of coho salmon in the Klamath basin began in the 1910-1911 season and continued for another 5 yr. From 1919 to 1942, six additional plants of hatchery-reared fish, all apparently of local origin, were conducted (CDFG 2002). The principal hatcheries today are the Iron Gate Hatchery (operating since 1966) on the Klamath and the Trinity River Hatchery (operating since 1963) on the Trinity River. Faced with a declining egg supply, operators of the two hatcheries at various times brought in fertilized eggs from the Eel and Noyo rivers in California and the Cascade and Alsea rivers in Oregon (CDFG 2002). Thus, present hatchery stocks probably are of mixed origin. Although a few hatchery fish have been planted in tributaries, hatchery fish are for the most part released as smolts into the main stem on the assumption that they will head directly to the sea.

Genetic studies of the contribution of hatchery coho to wild populations in the Klamath basin are not available. Brown et al. (1994) inferred that most wild coho stocks in the basin were partially mixed with hatchery stocks because the two hatcheries are at the far upstream end of coho distribution and produce large numbers of fish. In recent years, the Trinity River Hatchery has released an average of 525,000 coho per year and the Iron Gate Hatchery about 71,000 per year (CDFG 2002), although historically the Iron Gate Hatchery has released about 500,000 coho per year (CDFG, unpublished data, 2002). The coho typically are reared to the smolt stage and marked with a maxillary clip before release, which occurs between March 15 and May 1. They reach the estuary in concert with wild smolts, which peak in late May and early June, but typically are longer than the wild fish—about 170-185 mm vs 135-145 mm (M. Wallace, CDFG, unpublished data, 2002). Although the effect of large numbers of hatchery coho on wild coho is not known for the Klamath, hatchery fish may dominate wild fish when the two are together (Rhodes and Quinn 1998). In any event, hatchery fish are apparently more numerous than their wild counterparts. In 2000 and 2001, 61% and 73%, respectively, of the smolts captured in the estuary were of hatchery origin (M. Wallace, CDFG, unpublished data, 2002).

The percentage of hatchery fish in the spawning population has not been estimated directly, but Brown et al. (1994) estimated that 90% of the adult coho in the system returned directly to the hatcheries or spawned in the rivers in their immediate vicinity. Other hatchery coho no doubt stray into other streams, but the percentage is not known (CDFG 2002). In a survey of spawning coho in the Shasta River in 2001, individuals from the Iron Gate and Trinity River hatcheries were identified; seven of 23 carcasses examined were hatchery fish (CDFG, unpublished data, 2001). Regardless of origin, natural-spawning coho in the basin's tributaries have managed to maintain timing of runs and other life-history features that fit the basin's hydrologic cycle well.

Status

Coho salmon populations in California in general and in the Klamath basin specifically have declined dramatically in the last 50 yr (Brown et al. 1994, Weitkamp et al. 1995, CDFG 2002). The Southern Oregon-Northern California Coast (SONCC) ESU, of which Klamath stocks are part, was listed as threatened by the National Marine Fisheries Service (NMFS) as a consequence. The California Department of Fish and Game (CDFG 2002) recommended listing the ESU as threatened under the California state endangered species act, and the recommendation was adopted by the Fish and Game Commission as official state policy. Analysis by CDFG (2002) suggests that SONCC populations have stabilized at a low level since the late 1980s but could easily decline again if stream conditions change. Surveys in 2001 indicated that 17 (68%) of 25 historical coho streams in the Klamath basin contained small numbers of juvenile coho (CDFG 2002). In the Trinity River, wild coho stocks have experienced reduction of about 96% (USFWS/HVT 1999). The role of coho spawners of hatchery origin in maintaining these populations is not known, but marked fish of hatchery origin have been found among the spawners.

CHINOOK SALMON

Chinook salmon were and continue to be the most abundant anadromous fish in the Klamath basin, and their management potentially influences the abundance of coho in the basin and vice versa. They support important commercial, sport, and tribal fisheries. Annual runs have ranged from about 30,000 to 240,000 fish in the last 25 yr (CDFG, unpublished data, 2002), although runs were much larger historically (Snyder 1931). Chinook salmon spawn and grow primarily in the main stem of the Klamath River, in the larger tributaries (such as the Salmon, Scott, Shasta and Trinity rivers), Bogus, Indian, Elk, and Blue creeks, and also in some smaller tributaries. Large numbers once spawned in the Williamson, Sprague, and Wood rivers above Upper Klamath Lake, but these runs were eliminated by the construction of Copco Dam in 1917 (Snyder 1931).

Two ESUs are recognized for Klamath basin Chinook: the Southern Oregon and Coastal (SOCC) ESU and the Upper Klamath and Trinity rivers ESU (Myers et al. 1998). The SOCC ESU consists only of fall-run Chinook that spawn in the mainstem Klamath roughly from the mouth of the Trinity River to the estuary and is tied to other runs in coastal streams from Cape Blanco, Oregon, to San Francisco Bay. The Upper Klamath and Trinity rivers ESU encompasses the rest of the Chinook in the basin, including Trinity River fish. It consists of three runs (fall, late fall, and spring). Runs are named for the season of entry and migration up the river, which is not necessarily the same as the spawning time. Thus, spring-run Chinook migrate upriver during the spring, but spawn in the fall. The spring run differs in its life history from other runs and diverges slightly from them genetically as well; it may merit status as a separate ESU (Myers et al. 1998). Because studies of Chinook salmon and fisheries in the Klamath basin do not separate fish from the two ESUs (e.g., Hopelain 2001, Prager and Mohr 2001), Chinook salmon are treated here as either fall-run or spring-run. The late fall-run Chinook in the basin is either extinct or poorly documented (Moyle 2002). The vast majority of the fish today are fall-run fish of both wild and hatchery origin.

Fall-Run Chinook Salmon

Life History of Fall-Run Chinook Salmon

Fall-run Chinook in the Klamath have the classic ocean type of life-history pattern: juveniles spend less than a year in fresh water (Healey 1991). This pattern allows the salmon to take advantage of streams in which conditions may become unfavorable by late summer (Moyle 2002). Adult Chinook salmon that have the ocean type of life-history pattern also typically spawn in the main channels of large rivers and their major tributaries. Historically, the fall run in the Klamath was known as a summer run because fish started entering the estuary and lower river in July, peaked in August, and were largely finished by late September (Snyder 1931). Today, the run peaks in early September and continues through late October (Trihey and Associates 1996; USFWS, unpublished material, 1998). The 2- to 4-wk shift in run timing suggests that the mainstem Klamath and Trinity rivers have become less favorable to adult salmon in summer, presumably because of high temperature (Bartholow 1995), or perhaps because of excessive harvest of early run fish. Even with the shift in timing, temperature during the time of the spawning run probably is stressful to the migrating salmon and may result in increased mortality of spawning adults. Literature reviewed by Bartholow (1995) suggests that temperatures under 14°C are optimal for adult migration and that chronic exposure of migrating adults to 17-20°C can be lethal, although they can endure temperatures as high as 24°C for short periods. McCullough (1999, p. 75), commenting on adult migration primarily with data from the Columbia River, concludes that spring Chinook migrate at 3.3-13.3°C, summer Chinook migrate at 13.9-20.0°C, and fall Chinook migrate at 10.6-19.4°C.

Fall-run Chinook reach upstream spawning grounds 2-4 wk after they enter the river; they then spawn and die (USGS 1998). In 2001, adult Chinook were first recorded entering the Shasta River on September 11; the run peaked on October 1, and 95% of the run had entered the system by October 27 (CDFG, unpublished data, 2001). In 1993-1996, spawning in the reach between Seiad Creek and within 40 mi of Iron Gate Dam on the main stem began in the second week of October, peaked in the last week of October, and was completed by the middle of November (USGS 1998). This spawning period coincides with declining temperatures, which by early November are within the optimal range for incubation of developing embryos (4-12°C); 2-16°C is the range for 50% mortality (Healey 1991, Myrick and Cech 2001).

Time to emergence from the gravel varies with the temperature regime to which the embryos are exposed. In the mainstem Klamath River, alevins can emerge from early February through early April, but peak times vary from year to year (USGS 1998). In the Shasta River, newly emerged fry have been captured as early as the middle of January (USGS 1998). After they emerge, fry disperse downstream, and many then take up residence in shallow water on the stream edges, often in flooded vegetation, where they may remain for various periods. As they grow larger, they move into faster water. Some fry, however, keep moving after emergence and reach the estuary for rearing (Healey 1991). This pattern seems to be common in the Klamath River, although the small juveniles in the estuary leave, apparently for the ocean, after only a few weeks (Wallace 2000). The time that juveniles spend in the estuary may depend on upstream conditions (Wallace and Collins 1997). When river conditions are relatively poor (for example, warm), the juveniles move into the estuary when smaller and stay there longer. In other systems, juveniles may live in the estuary through the smolt stage and this can be important for allowing juvenile Chinook of the ocean life-history pattern to grow to larger sizes before entering the ocean (Healey 1991). Juveniles are found in the Klamath estuary from March through September (the sampling season), over which time new fish constantly enter and older fish leave (Wallace 2000; unpublished data 2002).

Other juvenile fall-run Chinook rear in the river or large tributaries for 3-9 mo, but downstream movement is fairly continuous. During June and July, movement of wild fish may be stimulated by the release of millions of juvenile salmon from Iron Gate Hatchery; the hatchery fish probably compete with wild fish for space. An outmigrant trap set at Big Bar, near Orleans, for 10 yr (1991-2001) captured juveniles from late February through late August, although the trap was usually set only from early April through July (T. Shaw, USFWS, unpublished material, 2002). Time of peak catch varied from year to year but usually was between late May and the middle of July. Outmigrant traps on the Scott and Shasta rivers catch Chinook fry, parr, and smolts from early February through July in most years. Peak numbers occur in March or early April for the Shasta River and from the middle of April to the middle of

May in the Scott River. A survey of mainstem pools at the mouths of creeks in 2001 indicates that juveniles can be found in the main stem from January through September, but abundances are considerably reduced by August and September (T. Shaw, USFWS, unpublished material, 2002). Thus, there appears to be a steady movement of fish down the main stem throughout summer; the fry stay for various periods in the main stem at temperatures of 19-24°C. That pattern is consistent with the thermal tolerances of juvenile Chinook salmon, which can feed and grow at continuous temperatures up to 24°C when food is abundant and other conditions are not stressful (Myrick and Cech 2001). Under constant laboratory conditions, optimal temperatures for growth are around 13-16°C. Continuous exposure to 25°C or higher is invariably lethal (McCullough 1999). Juveniles can, however, tolerate higher temperatures (28-29°C) for short periods. Depending on their thermal history, fish in wild populations may experience high mortality at temperatures as low as about 22-23°C (McCullough 1999). In the lower Klamath River, the presence in late summer of refuges that are 1-4°C cooler than the main stem and lower temperatures at night may increase the ability of the fry to grow. The abundance of invertebrate food also makes the environment bioenergetically favorable, although intense intraspecific competition may occur around the refuge pools.

What limits the survival of Chinook fry in the main stem is not known. Food is apparently abundant, and summer temperatures, although potentially stressful, are rarely lethal. It is possible that shallow-water rearing habitat is limiting for fry, especially if there is competition for space with other salmonids, including hatchery-reared Chinook and steelhead (e.g., Kelsey et al. 2002). Fry (under 50 mm) require shallow edge habitat for feeding and protection from predators. Thus, increasing flows to increase edge habitat may be desirable for as long as small fish are present. Some fall-run Chinook apparently remain in the river long enough to become smolts before they migrate to the sea; the rest do not (migration to the estuary is known to occur without smoltification in some cases). Timing of migration may be critical. Baker et al. (1995) indicated that prolonged exposure of outmigrating smolts to temperatures of 22-24°C in the Sacramento River resulted in high mortality. Juvenile Chinook salmon that transform into smolts at temperatures over 18°C may have low ability to survive in seawater (Myrick and Cech 2001).

Once the Chinook are at sea, they grow rapidly on a diet of shrimp and small fish (Healey 1991). They can move widely through the ocean but typically are most abundant in coastal waters, where growth and survival are strongly influenced by ocean conditions. They return to the Klamath mainly as 3-yr-old fish, but jacks (2-yr-old males) and 4-yr-old fish also are common.

Hatcheries

Hatcheries for Chinook salmon have been operating continuously since 1917. Both the Iron Gate Hatchery and the Trinity River Hatchery produce large numbers of spring-run (13%) and fall-run (87%) juvenile Chinook of native stock (Myers et al. 1998). The hatcheries release 7-12 million juveniles into the river each year (about 70% from the Iron Gate Hatchery, all fall-run). The fish generally have been released over a 2-3 days in late May or early June and take

1-2 mo (mean, 31 days) to reach the estuary (M. Wallace, CDFG, unpublished data, 2002), although some fish probably remain in pools for most of summer. Smaller fish take longer than larger fish to reach the estuary, but because they are feeding and growing on the way downstream, all juveniles are about the same size when they reach it. About 40% of the juvenile fish in the estuary in 2000 were of hatchery origin (CDFG, unpublished data, 2000); this is presumably a fairly typical figure. Adult Chinook returning to the hatcheries are roughly one-third of the total run—30% in 1999, 44% in 2000, and 28% 2001 (CDFG, unpublished data, 2001). There has been an increase in the percentage of hatchery fish in the run in recent years—up from 18% in 1978-1982, and 26% in 1991-1995 (Meyers et al. 1998). Their contribution to natural spawning is not known, but estimates for the Trinity River suggest that it is roughly the same as the percentage of hatchery returns (Myers et al. 1998).

Status

The fall-run Chinook salmon in the Klamath basin overall probably has declined in abundance, but it is still the most abundant salmonid in the basin. In the first major study of Klamath salmon, Snyder (1931) stated that "the actual contribution of the river to the entire salmon catch of the state is not known, nor can it be known. . . . The fishery of the Klamath is particularly important, however, because of the possibility of maintaining it, while that of the Sacramento probably is doomed to even greater depletion than now appears." Snyder did not provide estimates of run sizes, but the river harvest alone in 1916-1927 was 35,000-70,000 fish (as estimated from Snyder's data showing an average weight of 14 lb/fish and a harvest of 500,000-1,000,000 lb each year). If, as Snyder's data suggest, the river harvest was roughly 25% of the ocean harvest in this period, annual total catches were probably 120,000-250,000 fish. This in turn suggests that the number of potential spawners in the river was considerably higher than the number spawning in the river today. Since 1978, annual escapement has varied from 30,000 to 230,000 adults. In both 2000 and 2001, runs were over 200,000 fish. If it is assumed that fish returning to the hatcheries are, on the average, 30% of the population and that 30% of the natural spawners are also hatchery fish, then roughly half the run consists of salmon of natural origin (including progeny of hatchery fish that spawned in the wild).

Additional evidence of decline is the exclusion of salmon from the river and its tributaries above Iron Gate Dam in Oregon, where fairly large numbers spawned, and the documented decline of the runs in the Shasta River. The Shasta River once was one of the most productive salmon streams in California because of its combination of continuous flows of cold water from springs, low gradients, and naturally productive waters. The run was probably already in decline by the 1930s, when as many as 80,000 spawners were observed. By 1948, the all-time low of 37 fish was reached. Since then, run sizes have been variable but have mostly been well below 10,000. Wales (1951) noted that the decline had multiple causes, most related to fisheries and land use in the basin, but laid much of the blame on Klamath River lampreys: the lampreys preyed extensively on the salmon in the main stem when low flows delayed their entry into the Shasta River.

In some respect, it is remarkable that fall-run Chinook salmon in the Klamath River are doing as well as they seem to be. Both adults migrating upstream and juveniles moving downstream face water temperatures that are bioenergetically unsuitable or even lethal. As explained later in this chapter, the vulnerability of the run to stressful conditions was dramatically demonstrated by the mortality of thousands of adult Chinook in the lower river in late September 2002.

Spring-Run Chinook

Life History

Like coho, spring-run Chinook have a stream type of life history, which means that juveniles remain in streams for a year or more before moving to the sea (Healey 1991). In addition, the adults typically enter fresh water before their gonads are fully developed and hold in deep pools for 2-4 mo before spawning. In California, this strategy allows salmon to spawn and develop in upstream reaches of tributaries that often are inaccessible to fall-run Chinook because of low flows and high temperatures in the lower reaches during fall (Moyle 2002). Major disadvantages of such a life-history pattern in the present system are that low flows and high temperatures during the adult and smolt migration periods can prevent the fish from reaching their destinations or greatly increase mortality during migration (Moyle et al. 1995, Trihey and Associates 1996).

Spring-run Chinook enter the Klamath system from April to July, although the fish that appear later apparently are mainly of hatchery origin (Barnhart 1994). The Chinook aggregate in deep pools, where they hold through September. Temperatures below 16°C generally are regarded as necessary for spring-run Chinook because susceptibility to disease and other sources of mortality and loss of viability of eggs increase as temperature increases (McCullough 1999). In the Salmon River, temperatures of pools holding spring-run Chinook often exceed 20°C (West 1991, Moyle et al. 1995). Spawning peaks in October. Fry emerge from the redds from March to early June; the fish reside through the summer in the cool headwaters (West 1991). Because most of the streams in which they reside also are likely to be used by juvenile coho salmon, interactions between the two species are likely (see O'Neal 2002 for information specific to the Klamath). Some juveniles may move down to the estuary as temperatures decline in October, although most do not move out until the following spring (Trihey and Associates 1996); they spend summer in the same reaches as the holding adults. More precise details of the life history of spring-run Chinook in the Klamath basin are unavailable.

Status

Spring-run Chinook may once have been nearly as abundant as fall-run Chinook in the Klamath basin. Perhaps 100,000 fish spread into tributaries throughout the basin, including the Sprague and Williamson rivers in Oregon (Moyle 2002). The Shasta, Scott, and Salmon rivers all supported large runs. Spring-run Chinook suffered precipitous decline in the 19th century caused by hydraulic mining, dams, diversions, and fishing (Snyder 1931). The large run in the Shasta River disappeared coincidentally with the construction of Dwinnell Dam in 1926 (Moyle et al. 1995). In the middle to late 20th century, the decline of the depleted populations continued as a result of further dam construction (for example, of Trinity and Iron Gate Dams) and, in 1964, heavy sedimentation of habitat that resulted from catastrophic landslides due to heavy rains on soils denuded by logging (Campbell and Moyle 1991). By the 1980s, spring-run Chinook had been largely eliminated from much of their former habitats because the cold, clear water and deep pools that they require were either absent or inaccessible. In the Klamath River drainage above the Trinity, only the population in the Salmon River and Wooley Creek remains; it has annual runs of 150-1500 fish (Campbell and Moyle 1991, Barnhart 1994). Numbers of fish in the area continue to decline (Moyle 2002). Because the Trinity River run of several thousand fish per year is apparently sustained largely by the Trinity River Hatchery, the Salmon River population may be the last wild (naturally spawning) population in the basin. The Trinity River Hatchery releases over 1 million juvenile spring-run Chinook every year, usually in the first week of June. Apparently, all spawners in the mainstem Trinity River below Lewiston Dam are of hatchery origin.

NMFS debated designation of the Klamath spring-run Chinook as a distinct ESU, but decided that it was too closely related to fall-run Chinook to justify separation (Myers et al. 1998). Nevertheless, the presence of genetic differences and of great differences in life history suggest that it should be managed as a distinct ESU (as was done for the Sacramento River spring-run Chinook) or as a distinct population segment. Protection and restoration of streams used by spring-run Chinook salmon would provide additional protection for coho salmon because the two salmon have similar temperature and habitat requirements.

STEELHEAD

Steelhead (anadromous rainbow trout) are widely distributed and common in the Klamath basin. They consistently co-occur with coho salmon in streams, and the juveniles of the two species can have strong interactions (e.g., Harvey and Nakamoto 1996). All populations are considered by NMFS to be part of the Klamath Mountains Province ESU. Besides having genetic traits in common, the populations share a life-history stage called the half-pounder, which is an immature fish that migrates to the sea in spring but returns to spend the next winter in fresh water (Busby et al. 1994, Moyle 2002). Two basic life-history strategies are recognized in the basin: summer steelhead (stream-maturing) and winter steelhead (ocean-maturing). Barnhart (1994) and Hopelain (1998) divide the winter steelhead further into early (fall-run) and late (winter-run), but the two forms have similar life histories and will be treated together here as winter steelhead.

Winter Steelhead

Life History

Winter steelhead are the most widely distributed anadromous salmonids in North America. Key factors in their success in a wide variety of habitats include an adaptable life history, higher physiological tolerances than those of other salmonids, and ability to spawn more than once (Moyle 2002). The flexibility in life-history pattern is reflected in the fact that most populations have juveniles that spend 1, 2, or 3 yr in fresh water and adults that spend 2-4 yr in the ocean and return one to four times to spawn. This variability virtually ensures that runs can continue through periods of adverse conditions unless the stream habitat becomes chronically unfavorable to survival of steelhead.

Winter steelhead enter the Klamath River from late August to February (Barnhart 1994). They disperse throughout the lower basin and spawn mainly in tributaries but also show some mainstem spawning. Snyder (1933) noted that fish entering the Shasta River in 1932 came in bursts of 2-3 days over a 7-wk period. Spawning, which can take place any time from January through April, apparently peaks in February and March. Mature fish first return to spawn after a year, at 40-65 cm; the smallest fish are those that spent a winter in fresh water as half-pounders (Hopelain 1998). Up to 30% of the mature fish spawn a second time, after another year at sea; up to 20% spawn a third time; and a very few a fourth time (Hopelain 1998).

Fry emerge from the gravel in spring and most (80-90%) spend 2 yr in fresh water before going to sea. The rest spend either 1 or 3 yr in fresh water (Kesner and Barnhart 1972, Hopelain 1998). The juveniles occupy virtually all habitats in the basin in which conditions are physiologically suitable. They can tolerate minimal depths and flows and so can be found in the smallest accessible tributaries and in the main river channels. Although spawning occurs mainly in tributaries, the juveniles distribute themselves widely, and many move into the main stem. For example, large numbers of parr have been observed moving out of the Scott and Shasta rivers in early July (W.R. Chesney, CDFG, unpublished reports, 2000, 2002). Habitat preferences change with size: bigger fish are more inclined to use pools or deep runs and riffles, and the larger juveniles prefer water at least about 50-100 cm deep with water-column velocities of 10-30 cm/s and deep cover (Moyle 2002). Juveniles feed primarily on invertebrates, especially drifting aquatic and terrestrial insects, but fish (including small salmon) can be an important part of the diet of larger individuals. Aggressive 2-yr-old steelhead (14-17 cm) often dominate pools.

A key to the success of steelhead in fresh water is their thermal tolerance, which is higher than that of most other salmonids. Preferred temperatures in the field are usually 15-18°C, but juveniles regularly persist in water where daytime temperatures reach 26-27°C (Moyle 2002). Long-term exposure to temperatures continuously above 24°C, however, is usually lethal. Steelhead cope with high temperatures by finding thermal refuges (springs, stratified pools, and so on) or by living in areas where nocturnal temperatures drop below the threshold of stress. Persistence in thermally stressful areas requires abundant food, which steelhead will shift their behavior to find. Thus, Smith and Li (1983) found that juvenile steelhead persisted in a small California stream in which daytime temperatures sometimes reached 27°C for short periods by moving into riffles where food was most abundant; these fish, however, were at their bioenergetic limits for survival. Overall, the ability of steelhead to thrive under the summer temperatures experienced in the lower Klamath and the different habitat requirements of juvenile steelhead of different sizes indicate that they will benefit from the expansion of habitat created by increased flows in the mainstem Klamath and tributaries, as long as water quality, especially temperature, remains suitable for them.

Steelhead juveniles become smolts and move into the estuary from early April to the middle of May (Kesner and Barnhart 1972). Small numbers continue to trickle into the estuary all summer (M. Wallace, CDFG, unpublished data, 2002). A majority of the early fish that return each year to the river in September are immature (half-pounders, 25-35 cm). These fish usually stay in the lower main stem of the Klamath through March before returning to the sea. This life-history trait allows the steelhead to consume eggs of the large numbers of Chinook salmon that enter the river at the same time (USGS 1998). Half-pounders that return to spawn in the following winter are much smaller (40-50 cm), however, than the first-time spawners that skipped the half-pounder stage (55-65 cm) (Hopelain 1998).

Hatcheries

The Iron Gate Hatchery produces about 200,000 and the Trinity River Hatchery about 800,000 winter steelhead smolts per year (Busby et al. 1994). The fish are released into the rivers in the last 2 wk of March, and most reach the estuary about a month later (M. Wallace, CDFG, personal communication), coincident with the emigration of wild smolts. Diets of outmigrating smolts are similar to those of wild smolts, although the consumption of a greater variety of taxa and fewer organisms by the hatchery fish than by wild fish suggests that they have lower feeding efficiency than wild fish (Boles 1990). Otherwise, the interactions between hatchery and wild fish in the Klamath are not known, although hatchery steelhead released into a stream will dominate the wild steelhead (McMichael et al. 1999), potentially increasing the mortality in wild fish from predation, injury, or reduced feeding. Hatchery steelhead also can have adverse effects on juveniles of other salmonids, especially Chinook and coho salmon, through aggressive behavior and predation (Kelsey et al. 2002).

In the 1970s and early 1980s, adults of hatchery origin made up about 8% of the run of Klamath River steelhead and 20-34% of the run in the Trinity River (Busby et al. 1994). As numbers of wild steelhead decline, the percentage of hatchery fish in the population presumably will increase. There is some indication that the runs most heavily influenced by hatchery steelhead in the Trinity River have a lower frequency of half-pounders in the population than do wild populations (Hopelain 1998).

Status

Historical numbers of winter steelhead in the Klamath River are not known, but total run sizes in the 1960s were estimated at about 170,000 for the Klamath and 50,000 for the Trinity (Busby et al. 1994). Historical numbers for the Klamath River above the Trinity undoubtedly were much higher because by 1917 all access to the upper basin was eliminated and habitat in the tributaries was greatly degraded or blocked. In the 1970s, Klamath River runs were estimated to average around 129,000; by the 1980s, they had dropped to around 100,000 (Busby et al. 1994). Similar trends were noted for the Trinity River. Numbers presumably are still declining, although all estimates of abundance, past and present, are very shaky. NMFS considered winter steelhead in the Klamath to be in low abundance and to be at some risk of extinction (Busby et al. 1994) but has not listed them under the ESA.

Summer Steelhead

Life History

Summer (spring-run) steelhead have the same relationship to winter steelhead that spring-run Chinook salmon have to fall-run Chinook salmon in the Klamath River. They are closely related but have different life histories. Summer steelhead enter the Klamath River as immature fish from May to July and migrate upstream to the cool waters of the larger tributaries (Barnhart 1994, Moyle 2002). They hold in deep pools roughly until December, when they spawn. Temperature requirements of adult summer steelhead are not well documented, but maximum daytime temperatures of less than16°C seem to be optimal, and temperatures above 20°C increase stress substantially (Moyle et al. 1995) through susceptibility to starvation (they do not feed much while holding) and disease. High temperatures also decrease viability of eggs inside the females. Juveniles probably occupy mainly the same upper stream reaches in which they were spawned, that is, above the areas in which most winter steelhead spawn and rear but where coho are likely to be present. Other aspects of their life history are similar to those of winter steelhead, including a predominance of 2-yr-old smolts and the presence of half-pounders (Hopelain 1998). There is some evidence, however, that summer steelhead have higher repeat spawning rates and grow larger in the ocean (Hopelain 1998). As is the case with spring-run Chinook salmon, major disadvantages of the summer steelhead's life-history pattern in the present system are that reduced flows and increased temperatures during the adult and smolt migration periods prevent the fish from reaching their destinations or greatly increase their mortality during migration (Moyle et al. 1995, Trihey and Associates 1996).

Status

Summer steelhead once were widely distributed in the Klamath and Trinity basins and were present in most headwaters of the larger tributaries (Barnhart 1994). In the 1990s, estimated numbers were 1000-1500 adults divided among eight populations; the largest numbers were in Dillon and Clear creeks (Barnhart 1994, Moyle et al. 1995, Moyle 2002). Numbers presumably are still declining because of loss of habitat, poaching in summer, and reduced access to upstream areas during migration periods as a result of diversions. Summer steelhead and winter steelhead probably are different ESUs. NMFS considers the stocks depressed and in danger of extinction (Busby et al. 1994). Summer steelhead are not produced by Klamath basin hatcheries.

OTHER FISHES

Pink Salmon

Small runs of pink salmon probably once existed in the Klamath River and elsewhere on the coast. The pink salmon now appears to be extirpated as a breeding species in California, although individuals stray occasionally into coastal streams (Moyle et al. 1995, Moyle 2002).

Chum Salmon

Periodic observations of adult chum salmon and the regular collection of small numbers of young suggest that this species continues to maintain a small population in both the Klamath and Trinity rivers (Moyle 2002). It was more abundant in the past and occasionally was harvested, but it has never been present in large numbers. The run in the Klamath basin is the southernmost of the species. The life history of this species in the Klamath basin, including timing of spawning runs and outmigration of juveniles, is probably similar to that of fall-run Chinook salmon.

Coastal Cutthroat Trout

Because of their similarity to the more abundant steelhead, coastal cutthroat trout have been largely overlooked in the Klamath basin. They occur mainly in the smaller tributaries to the main stem within about 22 mi of the estuary. They also have been observed further upstream in tributaries to the Trinity River (Moyle et al. 1995). Their life history in the Klamath River is poorly documented but is apparently similar to that of winter steelhead. Adults enter the river for spawning in September and October, and juveniles grow in the streams for 1-3 yr before going to sea. Cutthroat trout can spawn two to four times. Competition for space by spawners and juveniles with the dominant steelhead is reduced by the ability of cutthroat to use habitats higher in the watersheds than are typically used by steelhead (Moyle 2002). Voight and Gale (1998) suggest that in small tributaries in the lower 22 mi of the Klamath River, cutthroat may actually be more abundant in headwater streams than they were historically because they have become resident above migration barriers created by human activities, such as log jams and debris flows. The life history of one such population on the nearby Smith River is documented by Railsback and Harvey (2001).

The general absence of cutthroat trout from streams higher in the Klamath basin presumably results from their general intolerance of water that exceeds 18°C (Moyle 2002) and from competition with the more tolerant steelhead and perhaps other salmonids. Juveniles move downstream when they reach 12-20 cm during April through June, coincidentally with the outmigration of juvenile Chinook salmon, a major prey (Hayden and Gale 1999, Moyle 2002). Adults apparently do not move far once they reach salt water and some may return to overwinter in fresh water; others may move up in summer. Movements into fresh water by nonbreeding fish may be triggered by abundance of juvenile salmon, which are prey; the timing of such movements into the lower Klamath appears to vary greatly from year to year (Gale et al. 1998). Large numbers of adult cutthroat are observed every summer in lower Blue Creek, where they seek refuge from poor conditions in the mainstem Klamath (Gale et al. 1998).

Eulachon

The eulachon or candlefish is a smelt (Osmeridae) that reaches the southern extent of its range in the Mad River, Redwood Creek, and the Klamath River (Moyle 2002). Historically, large numbers entered the river to spawn in March and April, but they rarely moved more than 8 mi inland. Spawning occurs in gravel riffles, and the embryos take about a month to develop before hatching and being washed into the estuary as larvae. The eulachon in the Klamath River once was an important food of the American Indians in the region (Trihey and Associates 1996). Since the 1970s, their numbers have been too low in most years to support a fishery. The causes of the decline are not known but probably are tied to changing ocean conditions and poor habitat and water quality in their historical spawning areas (Moyle 2002).

Green Sturgeon

Probably 70-80% of all green sturgeon are produced in the lower Klamath River and Trinity River, where several hundred are taken every year in the tribal fishery, which is the principal source of life-history information on this species (Moyle 2002). Green sturgeon enter the Klamath River to spawn from March to July; most spawning occurs from the middle of April to the middle of June at temperatures below 14°C. Spawning takes place in the lower main stems of the Klamath and Trinity rivers in deep pools with strong bottom currents. Juveniles occupy the river until they are 1-3 yr old, when they move into the estuary and then to the ocean. Optimal temperatures for juvenile growth in the river appear to be 15-19°C. Temperatures above 25°C are lethal (Mayfield 2002). After leaving the river, green sturgeon spend 3-13 yr at sea before returning to spawn and often move long distances along the coast. They reach maturity at 130-150 cm and are repeat spawners. Large adults (250-270 cm) typically are females that are 40-70 yr old (Moyle 2002). There is some evidence that green sturgeon populations are in decline, but reduction of the marine commercial fishery for them may have alleviated the decline somewhat (Moyle 2002). In 2003, NMFS rejected a petition to have them listed as a threatened species.

Pacific Lamprey

Lampreys once were so abundant in the coastal rivers of California that they inspired the name Eel River for the third largest river in the state. They supported important tribal fisheries. Today, their numbers are low and declining (Close et al. 2002, Moyle 2002). Their biology is poorly documented, but they probably have multiple runs in the Klamath basin. Most adults (30-76 cm) enter the river from January through March to spawn from March to June, although movement has also been observed in most other months (Moyle 2002). How far upstream lampreys moved historically is not known, but it is certain, as shown by the genetics of resident lampreys, that they entered the upper basin above Klamath Falls at least occasionally. Most spawning appears to take place in the main stem or larger tributaries. Like salmon, lampreys construct redds for spawning in gravel riffles, although the tiny larvae emerge from the gravel in just 2-3 wk. They are washed downstream once they emerge, and they settle in sand and mud at the river's edge. The larvae (ammocoetes) live in burrows in these quiet areas for probably 5-7 yr and feed on algae and other organic matter. During the larval stage, they move about frequently, so they are commonly captured in salmon outmigrant traps. Factors limiting the survival of ammocoetes are not known, but it is likely that rapid or frequent drops in flow deprive them of habitat and force them to move into open water, where they are vulnerable to predation. They do not appear to be limited by temperatures in the basin, but anything that makes their shallow-water habitat less favorable (such as pollution and trampling by cattle) is likely to increase mortality.

The blind, worm-like ammocoetes undergo a dramatic transformation into eyed, silvery adults when they reach 14-16 cm, after which they migrate to the sea (Moyle 2002). Downstream migration usually is coincidental with high flows in the spring, but movement has also been observed during summer and fall (Trihey and Associates 1996). In the ocean and estuary, they prey on salmonids and other fish for 1-2 yr before returning to spawn. The Pacific lamprey is a tribal trust species with a high priority for recovery to fishable populations (Trihey and Associates 1996). Its cultural importance to American Indians is largely unappreciated (Close et al. 2002).

Native Nonanadromous Species

Speckled dace, Klamath smallscale sucker, lower Klamath marbled sculpin, threespine stickleback (some of which are anadromous), and Klamath River lamprey are quite common in the lower river and its tributaries of low gradient. With the possible exception of the sculpin, these species probably all have fairly high thermal tolerances (Moyle 2002). In the reaches within 30 mi or so of the ocean, marbled sculpin apparently are replaced by the two amphidromous species, prickly sculpin and coastrange sculpin. With the exception of the lamprey, which feeds on fish, all the resident fishes feed mainly on aquatic invertebrates. The relationship between the native nonanadromous and anadromous species has not been worked out in the Klamath, but the dace, stickleback, sculpins, and suckers are probably subsidized by nutrients brought into the streams by the anadromous fish and may suffer heavy predation, especially in the larval stages, by juvenile salmon and steelhead.

Nonnative Species

The lower Klamath basin is still dominated by native fishes, but other species have a strong presence in highly altered habitats, such as reservoirs and ponds. The Shasta River, once a cold-water river, now supports large populations of brown bullheads and other warmwater, nonnative species because summer flows consist largely of warm irrigation-return water. There also is a continuous influx of nonnative fishes from the upper Klamath basin, where they are extremely abundant. Because there is a positive relationship between degree of habitat disturbance and abundance of nonnative fishes (Moyle and Light 1996), improving habitat for native fishes should reduce the likelihood that nonnative species will become more abundant.

MASS MORTALITY OF FISH IN THE LOWER KLAMATH RIVER IN 2002

During the last half of September 2002, mass mortality of fish (fish kill or fish die-off) occurred in a reach of the Lower Klamath River extending about 30 mi up from the confluence of the river with its estuary (Figure 1-1). In responding to the general need for a timely assessment of the conditions leading to this mortality, CDFG released in January 2003 a report that describes the extent of the mortality and its distribution among species, hydrologic and meteorological conditions that accompanied the mortality, some aspects of water quality, and the results of physical examination of both living and dead fish. A second CDFG report will deal with long-term consequences of the mortality. Also during 2003, USGS released a report dealing with the mortality of September 2002 (Lynch and Risley 2003). The USGS report documents environmental conditions that coincided with the mortality, but does not attempt to reach conclusions as to its cause.

The sponsors of the NRC study on endangered and threatened fishes asked the NRC Committee to study information on the fish kill of 2002 and include the analysis in its final report. While it is reasonable that this issue be covered in the committee's report, it is also important to note that the fish kill primarily affected Chinook salmon, for reasons that are explained below, and not the threatened coho salmon that is the focus of attention for the NRC Committee in its work on the lower Klamath basin. Furthermore, the NRC Committee was only able to consider the two reports cited above and unpublished records on weather and temperature; other reports to be issued in the future might provide additional information that would influence conclusions about the cause of the fish kill. The fish kill of 2002 in the Klamath lower main stem is unprecedented in magnitude. It raises questions as to whether human manipulation of the Klamath River or the adjoining estuary was directly or indirectly responsible and, if so, what might be done to prevent its recurrence. A full and final explanation of mortality probably is not possible, however, given that the fish kill was not anticipated and therefore the conditions leading to it were not well documented.

Extent of Mortality

CDFG, quoting USFWS, has estimated the total mortality of fish in the last half of September 2002 at about 33,000. This estimate, which is subject to revision, is likely to be conservative. The projected run size of fall-run Chinook salmon, which was the most abundant of the fish that died, was estimated at 132,000. Thus, regardless of any adjustments that might be made in the final estimate of mortality, a substantial portion of the Chinook salmon run was lost before spawning.

Both CDFG and USFWS estimated the species composition of the fish kill, which extended beyond salmonids to other taxa, including the Klamath River smallscale sucker, but percentage estimates from CDFG are limited to the salmonids. A sample of 631 dead fish collected under the supervision of CDFG showed 95.2% Chinook salmon, 4.3% steelhead trout, and 0.5% coho salmon. These estimates differ only slightly from the USFWS estimates. Further details may appear in reports yet to be issued. Among both Chinook and steelhead, nonhatchery fish appeared to have died in greater numbers than fish of hatchery origin. A similar determination for coho salmon is complicated by the fact that only small numbers of coho were found. If the coho had been in peak migration at the time when mortality occurred, more dead coho probably would have been found. The coho migration occurs later than the Chinook migration, which probably explains why few coho were affected.

Direct Causes of Mortality

CDFG has given infection as the direct cause of death of the fish. Both living and dead fish were infected with *Ichthyopthirius multifilis,* a protozoan, and *Flavobacter columnare,* a bacterium. As indicated by CDFG, these two pathogens are widespread and, when they become lethal to fish, typically are associated with high degrees of stress. Crowding may be considered an additive agent to stress in that it facilitates efficient transmission of pathogens from one fish to another. A combination of crowding and stress thus would be especially favorable for the development of these pathogens in sufficient strength to cause mortality of fish. Potential agents of stress, which may have acted in combination rather than alone, include high temperature, inadequate concentrations of dissolved oxygen (undocumented), and high concentrations of unionized ammonia (undocumented).

Indirect Causes of Mortality

Low flow in the Klamath River main stem is the most obvious possible cause of stress leading to the lethal infections of fish in the lower Klamath River during 2002. Low flow can cause crowding of the fish in their holding areas as they await favorable conditions for upstream migration and can be associated with high water temperature and with lower than normal concentrations of dissolved oxygen. CDFG therefore reviewed information on flow in the main stem, as did USGS (Lynch and Risley 2003).

The flow of the Klamath River at Klamath, which is just a few miles above the estuary, is shown in Figure 7-3 for dry yrs used by CDFG in its overview of low flows in the river. The flows at Iron Gate Dam, about 185 mi upstream, are given for comparison. For an extended span of years not restricted to drought, September flow at Iron Gate Dam is about one-third of the flow at Klamath. For example, mean September discharge at Klamath was 2973 cfs for 1988 through 2001 (excluding 1996, 1997) and the same statistic for the Klamath River at Iron Gate Dam is 1130 cfs, as determined from USGS gage records.

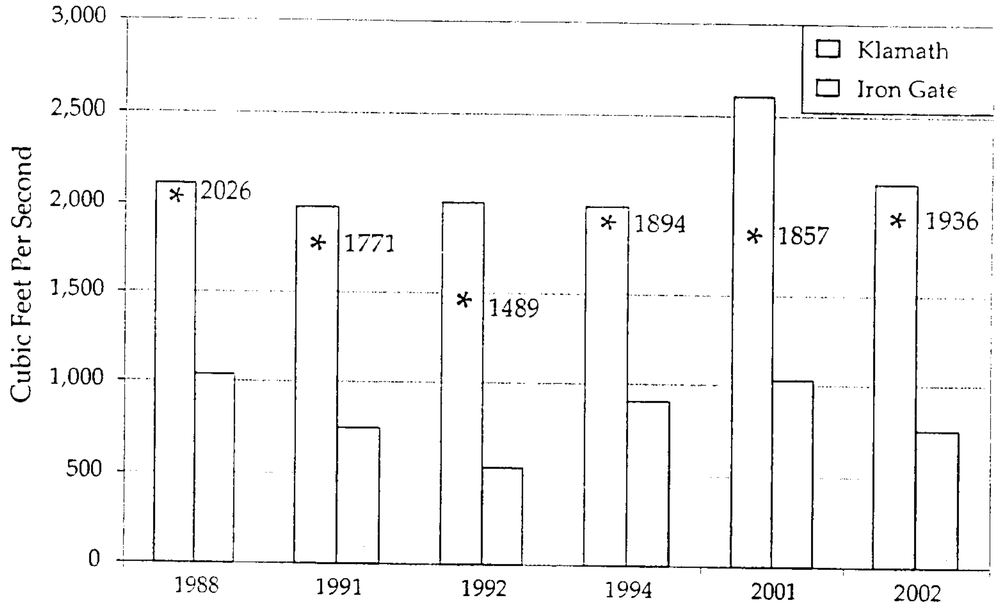

Figure 7-3. Mean flows of the Klamath main stem at Klamath (near the site of the 2002 fish kill) and at Iron Gate Dam (about 185 mi upstream) in September for 6 low-flow years considered by CDFG in its analysis of the fish kill. The asterisk shows the sum of flows for the Klamath at Orleans and the Trinity at Hoopa, as a check on the Klamath gage (this sum omits small tributaries below the Trinity). Sources: data from CDFG 2003 and USGS gages.

The USGS elected not to use data for the Klamath gage because the accuracy of the gage at low flow is subject to errors greater than 15%. Figure 7-3 shows the sum of the gages at Orleans (main stem above the Trinity) and at Hoopa (on the lower Trinity), both of which produce discharge readings within 10% of the true value, for comparison with the flows in the mainstem at Klamath. The two sets of values are separated by some additional discharge (undocumented) that accumulates below the Trinity. The Klamath gage data and the sum of the two gages above it show essentially the same picture qualitatively, as does the analysis by USGS based on the Orleans gage alone. Also, USGS restricted its analysis of flows to 1-24 September, which coincides better with observed mortality than 1-30 September, but the mean gage readings for these differing intervals are essentially identical (< 1% difference at Klamath). All data indicate that flows comparable with those of 2002 have occurred a number of times over the last 15 yr without causing mass mortality of salmonids. This does not rule out the possibility that low flow was a factor, but it does suggest that the occurrence of flows similar to those of 2002 has not in the past been sufficient by itself to cause mass mortality.

The USGS analysis adds a new dimension to future concerns related to flow in that it shows a substantial increase in distance to the water table over 2001 and 2002, both of which were dry years. Because shallow alluvial water reaches the tributaries and mainstem Klamath as ground water, which supports flow in dry weather, drawdown of the water table by pumping should be taken into account in any future evaluation of low flows, particularly if pumping is a growing response to water scarcity during drought. Flow could be related to crowding on a conditional basis through run size or timing of run. CDFG considered this possibility by using estimates of run timing and run size of Chinook salmon, which accounted for most of the fish biomass in the river during the last half of September. The analysis showed that the run of Chinook was only slightly larger than average and that it was bracketed by run sizes both smaller and larger for other comparably dry years. Thus, run size does not show evidence of being a conditional influence related to flow.

The August-October run of Chinook appears to have peaked earlier in 2002 than in other years of record, and this suggests a conditional relationship with low flow in causing mortality. CDFG was reluctant, however, to attribute great significance to this possible relationship, given the small amount of information on which it is based. The data available to CDFG indicated that air temperatures were not unusually high during September 2002 compared with other years of low flow when no fish kills occurred. Information on water temperature is sketchier, but also indicates that average maximum water temperatures fell within the range of water temperatures in previous years of low water when there were no fish kills. The USGS made comparisons of the Klamath River with the Rogue River, which is located nearby and has more comprehensive temperature records. Both water and air temperatures on the Rogue River were approximately 2°F higher in 2002 than the mean for the period of record. While the difference is small, the threshold for harm to salmonids lies close to September temperatures, even in years of average flow. The USGS analysis, like the CDFG analysis, did not suggest that temperatures in 2002 were extreme by comparison with other years of low flow when no fish kills occurred. Thus, if temperature is a factor governing mortality, it would involve coincidence of high temperatures with some other factor, the nature of which is not clear from the presently available information.

Tests of water quality did not indicate the presence of toxicants, although the water was not sampled until seven days after the onset of the first observation of dead fish (CDFG 2003). It is always possible that toxicants not tested were involved, but this seems unlikely, given that the fish kill occurred over an extended period and that there is no circumstantial evidence of the role of toxicants other than possibly ammonia generated by the fish themselves.

CDFG also considered fish passage. According to CDFG, high flows in 1997 and 1998 may have caused aggradation and expansion of channel bars that inhibited fish passage during extremes of low flow. These changes did not result in fish kills during the low-water year of 2001, but flows in 2001 were not as low as those in 2002. Thus, a current hypothesis of CDFG is that a change in channel geometry has created new conditions that are detrimental to fish at low flows even though such flows previously did not lead to high mortality. The hypothesis is speculative in that changes in channel conditions have not been established by measurement, but it should remain under consideration until further relevant evidence is collected.

Summary of Explanations

The possibility that passage is inherently more difficult at low flows now than it was before 1997-1998 was the only explanation of unique conditions leading to the fish kill that CDFG could not rule out in preparing its January 2003 report. Because of the limited data about conditions before and during the kill, other hypotheses probably will emerge as other reports are prepared. One hypothesis that has not been evaluated by CDFG involves the effect of temperature extremes during the fish kill. As explained earlier in this chapter, mean water temperature is less important for salmonids than extremes of water temperature. Thus, for example, the failure of temperatures to decline sufficiently at night when mean temperature is high could place unusual stress on salmonids but could be overlooked in a consideration of mean and maximum temperatures alone. Such conditions could occur, for example, when back radiation is so low (perhaps as a result of cloudiness or high humidity) that a typical amount of cooling would not occur at night.

A sequence of events involving daily minimum temperature rather than fish passage might be a cause of mortality. A large number of salmon moved up the river coincident with a series of days in which water temperatures were high enough to inhibit migration. McCullough (1999) states that, based on studies in the Columbia River, Chinook salmon cease migrating when maximum water temperatures exceed 21°C. Lynch and Risley (2003) indicate that during the time of the kill, maximum water temperatures in the river at Orleans, 30 mi upstream of the kill, averaged 20.3°C, and that the average minimum was 19.7°C. Thus it seems likely that temperatures in the Klamath River at the site of the kill reached or approached the inhibitory temperatures. As they commonly do, the salmon held in pools when the temperatures were high, waiting for conditions to improve before continuing upstream. The temperature and flow data given by Lynch and Risley (2003) indicate, however, that conditions did not improve and that nocturnal temperatures were not much lower than daytime temperatures. Because salmon are more vulnerable to infectious diseases at higher temperatures (McCullough 1999), crowding encouraged the disease outbreak that resulted in the kill.

The fish-passage hypothesis of CDFG or the minimum temperature hypothesis given above may or may not justify additional release of flow from Iron Gate Dam. It is unclear whether low flows actually blocked upstream migration or, as suggested by the literature, that most of the fish stopped moving because of high temperature (CDFG cites evidence that at least a portion of the run was capable of moving upstream during these low-flow conditions). The emergency release of 500 cfs of additional water from Iron Gate Dam by USBR, which arrived long after the fish kill had ended, lacked any specific justification. For relief of physical blockage, if it occurs, only a large amount of water (e.g., 1500 cfs) would be of use. Additional water from the Trinity could be especially valuable in that it would be cooler, if released in quantity.

If passage is the key issue, the recurrence of low flows similar to those of 2002 will probably be accompanied by mass mortality of fish. If other explanations, including minimum temperature, are the key explanation of mortality, recurrence is less likely, although higher temperatures over the long term caused by climate change could increase the likelihood that such kills would occur. Aggressive pursuit of some recommendations related to coho salmon (see information on augmentation of cold-water tributary flows in Chapter 8) could, if successful, reduce the risk of mass mortality of Chinook salmon. In any case, it is clear that increased monitoring of water quality and channel conditions in relation to flows in the lower main stem is needed in support of measures that may be necessary to prevent loss of Chinook salmon.

CONCLUSIONS

The lower Klamath basin is a geologically dynamic region that historically had large runs of anadromous fishes with diverse life histories. The fishes were widely distributed in the basin; some even entered the rivers that fed Upper Klamath Lake. The Salmon, Scott, Shasta, and Trinity rivers—all of which are major tributaries of the Klamath River—were major salmon and steelhead producers. The Shasta River in particular, with its cold flows and high productivity, was once especially productive for anadromous fishes. In the Klamath basin as a whole, Chinook salmon were and are the most abundant salmonid, followed by steelhead. Coho salmon rank third, but are well below Chinook and steelhead in abundance.

Virtually all populations of anadromous fishes have declined considerably from their historical abundances, although documentation for some species, such as Pacific lamprey and green sturgeon, is poor. Three of the most distinctive forms—coho salmon, spring-run Chinook, and summer steelhead—are on the verge of extinction as naturally maintained populations in the basin. It is significant that these three are the most dependent on summer water temperatures below 18°C and that they historically spawned and developed in tributary streams, many of which now are too warm for them. The anadromous fishes have been in decline since the 19th century when dams, mining, and logging severely altered many important streams and shut off access to the upper basin. The declines continued through the 20th century with the development of intensive agriculture with its dams, diversions, and excessively warm water both inside and outside the basin. Continued logging in headwater areas and commercial fishing also have contributed to the decline.

The mainstem Klamath River has become a challenging environment for anadromous fishes because of decreased flows and increased summer water temperatures. Although it is inhospitable to juvenile coho, it is still important for the rearing of juvenile Chinook salmon and steelhead, but increases in temperatures in July-September of 1-3°C may make it unsuitable even for them in the future. Increased flows down the river in summer are likely to benefit anadromous fishes only if temperatures can be kept within bioenergetically favorable ranges. This is particularly true for the lowermost reach of the main stem, below the Trinity River, which may be either cooler or warmer in late summer than the main stem, depending on the amount of water being released from Lewiston Dam.

Millions of juvenile fish, including Chinook salmon, steelhead, and coho are released into the Klamath and Trinity rivers each year by the Iron Gate and Trinity River hatcheries, which were built to mitigate salmonid losses created by large dams. These hatcheries have helped to maintain fisheries for coho and Chinook salmon, but their effect on wild populations of salmonids in the basin is not well understood. It is likely, however, that interactions between the hatcheries and wild juveniles in the river are having an adverse effect on the survival of wild juveniles through competition for space and food and aggressive interactions (e.g., McMichael et al. 1999, Kelsey et al. 2002), to the extent that the contributions of hatchery fish to fisheries are at least partially offset by the decreased contribution of wild fish (Levin et al. 2001). A high percentage of naturally spawning adult coho and Chinook salmon are of hatchery origin.

Native nonanadromous fishes are widespread and common in the drainage, but their relationships to anadromous fishes are not known. Nonnative fishes are uncommon in the lower basin except where drastically altered habitats favor them. If habitat degradation continues, the

Klamath River and its main tributaries will probably favor nonanadromous native and nonnative fishes increasingly at the expense of anadromous fishes. The hierarchical nature of watersheds assures that many environmental changes, some of which are quite small individually, collectively affect fish populations not only in their immediate vicinity but also both upstream and downstream because of the extensive movement of fishes (Fausch et al. 2002).

The problems with coho salmon are a reflection of larger problems with poor habitat and water quality for anadromous fishes generally in the basin. Restoration efforts that benefit coho salmon should benefit most, but not necessarily all, declining species. Prevention of further listings under the ESA requires a systematic, basin-wide approach to restoration and management. Some major gaps in knowledge are as follows:

1. Information on the biology of coho and other salmonids in the basin is largely unsynthesized; synthesis and interpretation of data on historical trends and present conditions would be especially valuable.
2. Studies on anadromous fishes other than fall-run Chinook, winter steelhead, and coho are very limited or lacking, particularly for summer steelhead, spring-run Chinook, and Pacific lamprey. It cannot be assumed that management strategies favoring species of primary interest also favor other species.
3. The biology of nonanadromous native fishes and macroinvertebrates in the basin is largely unknown, including basic descriptions of life histories and environmental requirements and their relationships to coho salmon and other anadromous fishes.
4. The potential effects of global climate change on the Klamath basin and its fishes, especially coho, are poorly understood, including the relationship between changing ocean conditions and the abundance of coho and other anadromous fishes. Climate warming would almost certainly be disadvantageous to coho.
5. The thermal consequences of stream and watershed restoration actions, including increasing summer flows down the mainstem Klamath River, are not well documented, especially in relationship to coho salmon.
6. The effects of hatchery operations on wild populations of coho and other salmonids in the basin are not understood, including the effects of hatchery steelhead and Chinook on juvenile coho salmon.
7. Strategies for improving tributaries for spawning and rearing of coho and other anadromous fishes are not yet well defined.
8. The lower 30-40 km of the mainstem Klamath seems to be increasingly unfavorable to anadromous fishes, for reasons that are not known. The effect on the lower river of changing flows from the Trinity River needs to be evaluated, as do the potential benefits of comanaging flow releases from the dams on the Trinity and Upper Klamath rivers.
9. Reliable abundance estimates and habitat affinities of juvenile coho and other salmonids are largely lacking.